

On the Distribution and Evolution of the Cyprinodont Fishes of the Mediterranean Region and the Near East

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(With 1 Map)

1. Species Records.

Records of the Cyprinodont fishes found at the present time in the Mediterranean region and the Near East include the following species*):
Subfamily: C Y P R I N O D O N T I N A E

1. Genus: *Aphanius* Nardo, 1827, [*Cyprinodon* Lac.]
 1. *A. burdurensis* F. Aksiray, 1948 [*Cyprinodon sureyanus* Neu ? ex parte] with 2 subspecies¹.
 2. *A. chantrei*, (Gaillard, 1895) [*C. blanfordi* Jenk., *C. persicus* Jenk.] with 11 subspecies¹.
 3. *A. cypris*, (Heckel, 1846) [*C. mento* Heckel] with 4 subspecies¹.
 4. *A. dispar* (Rüppell, 1826).
 5. *A. fasciatus* (C. V., 1846) [*C. calaritanus* C. V.]
 6. *A. ginaonis* (Holly, 1929)⁹.
 7. *A. iberus* (C. V., 1846).
 8. *A. sophiae* (Heckel, 1846) with 3 subspecies¹.
 9. *A. zaccarini* (Gianferrari, 1933) with 2 subspecies⁶.
2. Genus: *Anatolichthys* Kosswig and Sözer, 1945.
 10. *A. burdurensis* F. Aksiray, 1948 [*Cyprinodon sureyanus* new, ? ex parte].
 11. *A. splendens* Kosswig and Sözer, 1945.
 12. *A. transgrediens* F. Aksiray, 1948, with 11 distinct local populations¹.
3. Genus: *Tellia* Gervais, 1853.
 13. *T. apoda* Gervais, 1853.

Subfamily: F U N D U L I N A E

4. Genus: *Valencia* [*Fundulus* Lac.].
 14. *V. hispanica* (C. V., 1846).
 15. *V. letourneuxi* (Sauv.).
5. Genus: *Kosswigichthys* Sözer, 1942.
 16. *K. asquamatus* Sözer, 1942.

*) Three species are omitted from the list: *Cyprinodon danfordi* Boul., found only once, is of doubtful validity ¹¹. — *C. sureyanus* Neu has to be cancelled ¹. — *C. richardsoni* Boul., allegedly found in Lake Tiberias ², was probably misidentified.

2. Distribution.

The geographical distribution of the various species is shown in the appended sketch map. Additional remarks may aid in the understanding of the historical analysis which is to follow.

Three species of the genus *Aphanius* *) are semi-marine in the sense that coastal waters are their main routes of migration and distribution, while marine- or brackish-water canals, coastal rivers and their estuaries, lagoons, salt pools, etc., are their favoured habitats and breeding sites. The species concerned are: *A. dispar*, *fasciatus* and *iberus*. Although information on localities is incomplete it may be assumed that *fasciatus* occurs all along the Mediterranean coast (including that of the islands) from Eastern Algeria in the SW to the vicinity of Toulon in the NW. In the NE *fasciatus* inhabits the Sea of Marmora but appears to have penetrated no farther than Istanbul in the direction of the Black Sea. In the SE the species has successfully extended its area, since migration via the Suez Canal has brought it to Lake Timsah where it is abundant^{14, 21}. Nowhere does *fasciatus* approach the Atlantic Ocean. The westernmost stretches of the Mediterranean coast are inhabited by *iberus*¹⁷, which may thus be considered the geographical counterpart of *fasciatus*. There are, indeed, no records of *fasciatus* from the Moroccan or Iberian coasts; but a reciprocal penetration of both species in the respective border area may occur. A systematic analysis of border populations is highly desirable, especially in the light of the interesting reports⁴ of crossings between *fasciatus* and *iberus*. Since hybrids are easily obtained, it is quite possible that border populations will be found to be genetically mixed. Such observations would also be of importance in the discussion of the evolution of these species.

A. dispar has been found on the coast of the Red Sea and the adjoining coast of the Indian Ocean as far as Cutch¹³. Within this area, *dispar* appears to behave like *fasciatus*. Recently, the species has extended its domain into the Mediterranean Sea, taking advantage of the Suez Canal. The steady progress of *dispar* has been noted by several authors. Occasional specimens were reported from Port Said as early as 1904³. Final establishment in the Mediterranean was reported more than four decades later¹²: *dispar* now reproduces regularly in Athlit, about 370 km north-eastward, along the coast, from Port Said. This coastal stretch and, farther south, the Suez Canal to Lake Timsah is common ground for *dispar* and *fasciatus*. As early as 1927 it was already suggested¹⁴ that these species may cross freely in Lake Timsah.

In addition to its marine area, *dispar* has a few entirely landlocked populations. Several localities in the Jordan- and Dead Sea Valley were

*) Two species, *A. ginaonis* from Persia, and *A. zaccarinii* from the Gulf of Aden, are excluded from the present review because the writer had no access to the papers dealing with them.

early recorded, some of them apparently erroneously. At least 2 isolated populations exist in that region, one at Ein Feshkha ^{19, 22} on the NW-coast, and the other on the SW-coast ²² of the Dead Sea *).

To our knowledge the remaining species of *Aphanius* have no essential relations to marine conditions. They are found in the Eastern Mediterranean countries and in the Near East (Iraq and Persia). The most extensive distribution areas are those of *cypris* and *sophiae* which will be considered jointly for reasons explained below. The vast area shown on the map is particularly well supported at numerous localities in SE-Anatolia, Syria, Lebanon, Israel and the westernmost part of Jordan. Other widely scattered localities with sporadic records are: Mosul, Bagdad and Nemek-Deria near Shiraz.

Southern Anatolia is exceptionally rich in Cyprinodontinae having no less than 5 strictly endemic species in addition to those already mentioned. *A. chantrei*, with its 11 subspecies inhabits a fairly large area closely adjoined to the considerably smaller area of *burdurensis*, with 2 subspecies. The 3 species of the endemic genus *Anatolichthys*, *A. burdurensis*, *splendens* and *transgrediens* occupy a small, more or less coherent area, every species quite isolated from one another.

The monospecific genus *Tellia*, represented by *T. apoda*, is similarly restricted in its distribution. It is the only genus endemic to the western part of the Mediterranean. Only two localities are on record ⁴ for the species, both high among the plateaus of the eastern Atlas range.

Some uncertainty prevails about the distribution area of the genus *Valencia*, subfam. Fundulinae, since clear-cut records of recent date are lacking. — *V. letourneuxi* is known from Crete (and ? Corfu ¹³); and *hispanica* from several Iberian localities (see map).

The second genus of the Fundulinae occurring in this region is the monospecific *Kosswigichthys*, endemic in Anatolia, where the species *asquamatus* lives. It has been found only in a single locality ¹⁸.

3. Biological and Systematic Relations

Among the 7 species of *Aphanius*, discussed here *, there are 5 (*dispar*, *fasciatus*, *iberus*, *cypris*, *sophiae*) which can obviously be referred to two different groups. The first group comprises the morphologically similar *dispar*, *fasciatus*, *iberus*, some common colour features of which are especially significant. The similarity between *dispar* and *fasciatus* has been repeatedly emphasized ^{10, 20}. Most of the authors report that they are able to distinguish the females of these species from one another, but with diffi-

*) Another continental locality, in Anatolia, has recently been rejected ¹¹.

*) See footnote, p. 114.

culty. As eminent an ichthyologist as Günther reported *fasciatus* from North Africa under the name of *dispar*⁷. Published descriptions of *A. iberus* are also very similar to the preceding species. In this connection we may recall what has been said above on the possibility of the overlapping of the ranges of *fasciatus* and *iberus* in border areas and on the artificial hybrids obtained from them. It is further important to remember the suggestion of Norman¹⁴ that *fasciatus* and *dispar* may cross freely where they meet. The biological aspect of this *Aphanius* subgroup is likewise noteworthy. The coastal migratory habits and the predilection for the described biotopes are more or less common to all three species. The experience of the author and his colleagues leads them to conclude that *dispar* and *fasciatus* are extremely euryhaline fishes, apt to live and reproduce in highly concentrated sea water **) (salt pans of Athlit, Israel: *dispar*; Limassol Salt Lake, Cyprus: *fasciatus*). While *fasciatus* also occurs in pure freshwater, we know of no similar habit of *dispar*. *A. iberus*, however, is reported to resemble *fasciatus* in this respect, inhabiting freshwater as well as concentrated salines. With regard to temperature preferences, *fasciatus* is fairly eurytherm: it is common in the warm SE-Mediterranean (even penetrating the Suez Canal), but not less so in the much cooler Sea of Marmora and in the Adriatic Sea. *A. iberus* may be less eurytherm and cannot be very thermophilous, as shown by its geographical distribution. In contrast *A. dispar* is a definitely thermophilous species. This follows not only from its Indo-Erythrean distribution or its occurrence in the thermal waters of the Dead Sea Valley; it can be observed quite easily in aquarium cultures of the fish, which have to be artificially heated even during the mild winter of Tel Aviv *). The significance of this character is discussed below.

The second subgroup of *Aphanius* includes *cypris* and *sophiae*. These two forms are so similar morphologically that disputes on allegedly misidentified specimens of this group constantly arise. Teeth, body proportions, colouration, fin counts, etc., have all been proposed as distinguishing characters, singly or in combination, without however, silencing criticism. New difficulties arose when it was discovered that, on the one hand, populations from isolated localities differed so markedly as to necessitate the creation of separate systematic entities; while on the other hand, *cypris* and *sophiae* were reported as living together in identical localities (Ataibé, Syria¹⁵; Ak göl, Anatolia⁸). The most recent attempt to overcome these systematic difficulties was made by F. Aksiray¹, who divided the Anatolian forms of *cypris* into 4 subspecies and those of *sophiae* into 3. The various populations of Syria, Lebanon, Israel, etc., are not taken in account by

**) Measurements of salinity are not available.

*) Personal communication from my colleague, Dr. H. Mendelsohn.

this subdivision. Moreover, the special problem of the mixed populations of Ataibé is not even touched. Aksiray himself points out the extreme systematic difficulties, and the solution he proposes is, on the whole, not very convincing. To the writer it seems not at all improbable that a thorough revision of *cypris-sophiae* based on the study of material from all countries concerned may lead to the conclusion that a considerable number of systematic entities must be maintained and/or created, while the repartition of these entities into two separate species may no longer be justified. As to the behaviour of these fishes, two more or less clearly developed trends exist, one of relative euryhalinity (if not halophily) together with thermophily; and another of preference for pure freshwater and lower temperature. Some authors (including the writer and his colleagues) have been accustomed to relate *sophiae* to the thermo-halophilous trend and *cypris* to the other.

Apart from the morphological and ecological characters which unite the *dispar-group* on the one, and the *cypris-group* on the other hand, there is an additional important factor which points to the same basic subdivision of the genus *Aphanius*: viz., the only attempts to cross members of the two groups, *fasciatus* × *cypris-sophiae*, have been unsuccessful *).

The two remaining species of *Aphanius* to be dealt with here, the Anatolian *chantrei* and *burdureus*, form another third, group within the genus (called for convenience the *chantrei-group*). But similarity within the group, and common differential characteristics distinguishing it from the other groups are not sufficient to characterize the *chantrei-group*. Genetic relations between *chantrei* and *burdureus* and between them and other Cyprinodonts of Anatolia are at present under investigation in the Department of Zoology of the University of Istanbul. The results obtained to date indicate rather complicated genetic conditions. It seems very probable that their continuing analysis will throw new light upon this *Aphanius* group as well as on the species of *Anatolichthys* (Prof. Kosswig, Istanbul, in litt.). This strange genus has been defined with regard to its scale cover as follows¹: Scales overlap but little or not at all; mostly not fully developed on the whole body; those of middle longitudinal row partially lacking, or, when present up to completeness, numbering more than 30 in majority of specimens *).

The monospecific genus *Tellia* differs from *Aphanius* primarily in its lack of ventral fins. It is important to recall that crossings in both direc-

*) I am indebted to Prof. Kosswig for his permission to make use of this information.

*) The wording is quoted almost verbally.

tions were obtained from *Tellia apoda* × *A. fasciatus* and *T. apoda* × *A. iberus*^{4**}).

Very little can be said of the representatives of the Fundulinae in the region discussed here. The descriptions of Valencia are not very informative. The biotopes inhabited by the two species, lagoons and similar sea-connected waters, freshwater, coastal or landlocked waters, are also not clearly defined. — *Kosswigichthys asquamatus* lives in a brackish inland lake. The total lack of scales in this fish is a very remarkable character, observed so far as is known to us only in this unique genus of the Cyprinodont fishes of the world. It is surprising that in Anatolia one entirely scale-less species of the Fundulinae occurs while three species of the genus *Anatolichthys* of another subfamily exhibit various degrees of scale reduction from fully scaled fishes to almost scale-less ones. As the genetic implications of this situation are at present under investigation (Prof. Kosswig, Istanbul, in litt.) any further discussion of the problem would serve no useful purpose at this point.

4. Fossil Records

A review of the literature shows that 3 fossil genera have so far been discovered. One fossil species has been referred to *Cyprinodon* which is mainly known as recent. The fossil genera are *Prolebias* Sauvage, *Pachylebias* Woodward and *Brachylebias* Priem.

The following 10 species of *Prolebias* have been established: *arvernensis*, *cephalotes*, *brogniarti*, *furcatus*, *goreti*, *gregatus*, *meyeri*, *pontaryensis*, *praecursor* and *stenoura*. Some of these are found in considerable numbers and in several places. The recorded area of *Prolebias* covers Italy, France and SW-Germany. They made their appearance in the Oligocene and are found throughout this period and the whole of the Miocene. As their teeth are of conical form they may be regarded as Fundulinae.

Pachylebias is referred to the Cyprinodontinae since its teeth are crenulated. The species on record are: *crassicaudus*, *gobio*, *gandryi*, *racalmuti*. They were found in Italy, Sicily and Crete in deposits from the Miocene.

Cyprinodon is represented by *C. pygmaeus* from the Oligocene of France.

Brachylebias (2 species) is known from the Miocene, found near Lake Urmiah, in Persia. Its subfamilial affinity is not known to the author.

5. Evolution

Kosswig¹¹ has shown in the most convincing way, that the Cyprinodonts occurring in Anatolia are best interpreted as Tethysrelicts. Zoogeo-

**) All hybrids obtained from *T. apoda* with *A. fasciatus* and with *A. iberus* lacked ventral fins. — It is noteworthy in this connection that all species of the Orestiatinae, another subfamily of the Cyprinodontidae, and *Empetrichthys* of the Fundulinae are also distinguished by the absence of the ventral fins.

graphical as well als ecological considerations led him to his conclusion. It is easy to see that such considerations likewise pertain to the rest of the Mediterranean and circummediterranean species (including *A. dispar*) which were not discussed by him. Furthermore, the paleontological evidence quite obviously confirms Kosswig's viewpoint. It is in the tertiary Tethys area that all the known Eurasiatic fossil Cyprinodonts have been found.

It should thus be interesting to determine what can be said of the geological age and the evolution of the recent representatives of the family in our region.

Cyprinodontinae: *Aphanius*. — In view of the fossil find of *Cyprinodon pygmaeus*¹⁶ the question immediately arises wether this species was already a true *Aphanius* (as used in the modern sense¹³) or wether it represents the ancestral stock common to *Cyprinodon s. s.* and *Aphanius*. The literature at my disposal does not permit any special commentary on this problem, which, however, has much actuality, since it will be shown that the genus *Aphanius* must be assumed to be of Tethys age.

Aphanius, which is found today in numerous geographically isolated and, to a certain extent, systematically differentiated populations, must have ben involved in the very process of the disappearance of the Tethys. The same process during Eocene, Oligocene and Miocene, closed the Mediterranean Tethys basin against the Indian part of that Sea due to the rise of land masses and the regression of the sea, and, at the same time, trapped the *Aphanius* populations of the coastal waters, of bays, rivers, etc., which were transformed into inland waters. The existence of representatives of the genus *Aphanius* in the Tethys is prerequisite to the understanding of its isolated occurrence at the present time in the Mediterranean, in the Indian Ocean and in many continental waters of the lands which developed in the course of the abovedescribed process.

It is obvious that, if representatives of the same species of *Aphanius* are met with today in localities which were separated by the rising lands that divided the Tethys, then the species itself must already have existed during that early era. This is exactly the situation of *A. dispar*. Found (before the opening of the Suez Canal) in the Red Sea and the Indian Ocean on the one hand, and in some springs of the Daed Sea Valley on the other hand, the species fully fits the definition of a Tethys relict. Its history since the days of the early Tertiary may tentatively be described as follows. With the close of the Mediterranean the area of *dispar* was dissected into two main parts, a north-western Mediterranean and a south-eastern Indian one. Between them some populations were trapped in inland waters of the

dividing continental barrier *). The deterioration of the climate in the later Tertiary caused considerable decrease in the temperature of the Mediterranean and, consequently, led to the extinction of many tropical animals. *A. dispar* in the Mediterranean was one of the victims. Most of the landlocked populations vanished in the course of these events, which also influenced conditions on the continent. The warm waters of the Dead Sea Valley constitute the last refuge of *dispar* in the North in the continent. In the Indian region an essential extension of its range coincided with the early Pliocene, when Indian waters flooded the Erythrean rift valley, bringing *dispar* with them finally to the Suez Gulf. Beyond this point the species did not extend until the most recent times, but it started to progress northward with the opening of the Suez Canal as described above.

A. fasciatus is probably not of Tethys age. Its distribution is purely Mediterranean. It has, further, no predilection for high temperatures. This, together with its definitely close relation to *dispar* suggests that it might be a descendent of *dispar*, adapted to the changed conditions of the Mediterranean in the outgoing Tertiary.

The evolution of *A. iberus*, may have followed one of two possible courses: it may have evolved from *dispar* simultaneously with and parallel to *fasciatus*; or have been derived later from *fasciatus*. Geographical details favour neither hypothesis over the other, but further anatomical study and genetical analysis may yield decisive evidence.

There is no anatomic and genetic objection to the conclusion that *Tellia* has sprung from an *Aphanius*-ancestor, which may have been one of the *dispar*-group, possibly *fasciatus*, or *iberus*. But, in principle, we should estimate its age as no greater than the period of its geographical isolation in the eastern Atlas Mountains.

Where should the ancestor of the *cypris*-group be sought? It has already been mentioned that all living populations of the group, isolated as they are, inhabit inland waters; even those occurring in coastal rivers have never been observed venturing into the sea. The range of the Tethys-*Aphanius* which gave rise to the recent *cypris*-group was perhaps less extensive than that of *dispar*. But it inhabited at least that part of the sea which then covered the lands in which its descendants are found today. Its range in Anatolia and Arabia was, in all probability, broader than in recent times; decreasing temperatures in the North and increasing aridity in the South having consequently limited its area. The evolution of such specialized populations as are found today is the outcome of the disruption of the uniform

*) A late *dispar* invasion, in the Lower Pliocene, when a marine gulf reached the upper Jordan Valley, seems improbable in the light of the cooling down of the Mediterranean waters discussed below. *A. dispar* could not have survived in the Mediterranean Sea until the late Pliocene.

coastal habitat of the Tethys into as many isolated biotopes differing one from another.

The evolution of the remaining *Aphanius* species, the *chantrei*-group, is under the consideration of the Istanbul zoologists, mentioned above, together with that of the genus *Anatolichthys*, and the subject will be left to them.

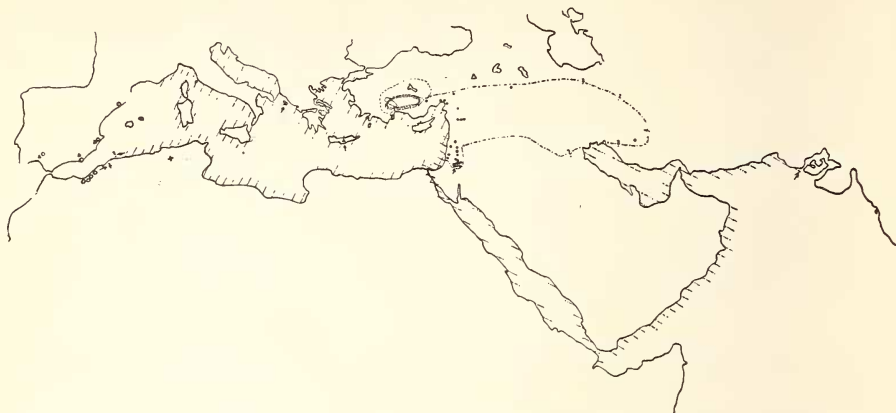
Fundulinae. The fossil records of this subfamily suggest that it was well established by a number of species at least in the European Tethys. The 3 recent species (belonging to two genera) are the relicts of a group which has declined markedly since the Oligocene, for which climatic condition may be primarily responsible.

The recent genera of *Valencia* and *Kosswigichthys* are very different from one another. Whereas the latter is highly specialized (absence of scales) and could have evolved only under protracted isolation, the former genus is of rather „generalized“ type and does not appear to have undergone considerable alteration. While this does not mean that *Valencia* is necessarily of Tethys age, it must be old enough for two separate species (*hispanica* and *letourneuxi*) to have derived from the common stem. The relation between *Valencia* and the fossil *Prolebias* is not yet elucidated¹³. The peculiarity of *Kosswigichthys* precludes the tracing of its origin by means of morphology and/or geography. But as the more specialized of the two genera it should be considered the younger of the two.

In conclusion it is certain, that both Cyprinodontinae and Fundulinae were inhabitants of the tertiary Tethys in the region discussed. The Fundulinae, well represented in early times, soon declined; surviving in one bispecific genus of typical habitus and, therefore, of relatively great age (*Valencia*), and one monospecific, specialized, and, therefore, relatively young genus (*Kosswigichthys*). In contrast the Cyprinodontinae flourished. The recent representatives *) derived from at least two ancient forms, which developed into about 5 species (*A. dispar*, *fasciatus*, *iberus*, *cypris-sophiae*, *T. apoda*), later splitting into many subspecific entities. Speciation in this subfamily has taken place at three levels. The earliest is the Tethys level including the differentiation of *A. dispar* and of the *cypris-sophiae* ancestor. The second, Mediterranean, level comprises the evolution of the marine and semi-marine species of *A. fasciatus* and *iberus*. The third is the continental level, including the development of the various forms of the *cypris-sophiae*-group, probably that of the inland form of *dispar*¹², and perhaps also that of *T. apoda*. While well-separated geographically, the second and third levels probably overlap in time. But at the third level activity still continued at a time when it had already ceased

*) *Aphanius chantrei* and *burduricus* and *Anatolichthys* excluded: see above.

at the second one. Opinions differ as to whether speciation at the third level is decreasing, or even concluded, or is still continuing undiminished.



Map: Distribution of Cyprinodont Fishes of the Mediterranean Region and the Near East

Explanation of Map

Coastal distribution of *Aphanius fasciatus*
 Coastal distribution of *Aphanius dispar*
 Distribution boundaries of *Aphanius cypris-sophiae*
 Distribution boundaries of *Aphanius chantrei*
 Distribution boundaries of *Aphanius burdurius*
 Distribution boundaries of *Anatolichthys*
 Localities of *Aphanius cypris-sophiae*
 Localities of *Aphanius dispar*
 Localities of *Tellia apoda*
 Localities of *Valencia*
 Localities of *Kosswigichthys*



Arrows point to isolated localities (*A. dispar* in the Dead Sea Valley, *Valencia* in Corfu and Crete) or to distribution limits (*A. dispar*, *A. iberus*, *A. fasciatus*).

Zusammenfassung

1. Die rezenten Arten der Cyprinodontidae des behandelten Gebietes gehören zu fünf Gattungen, verteilt auf zwei Unterfamilien. Cyprinodontinae sind mit 3 Gattungen und 13 Arten, Fundulinae mit 2 Gattungen und 3 Arten vertreten.

2. Drei *Aphanius*-Arten sind semi-marin: *A. dispar*, *fasciatus* und *iberus*. *Fasciatus* bewohnt die Mittelmeerküste mit Ausnahme der Pyrenäen-Halbinsel, wo *iberus* an seine Stelle tritt; *dispar*, eine indoerythraische Art, dringt durch den Suezkanal ins Mittelmeer vor, hat aber außerdem einige isolierte Populationen in Binnengewässern des Nahen Ostens. — Wo je zwei der genannten Arten sich treffen, kommen möglicherweise Hybriden vor. — *A. cypris* und *sophiae* bewohnen ein weites Gebiet in den östlichen Mittelmeer-Ländern, Iraq und Persien. — Anatolien hat fünf weitere Arten: *A. chantrei* (11 Unterarten), *A. burdurius* (2 Unterarten), *Anatolichthys burdurensis*, *splendens* und *transgrediens*. — *Tellia apoda* bewohnt zwei Gewässer im Atlasgebirge. —

Valencia ist mit *letourneuxi* aus Creta und mit *hispanica* aus Spanien gemeldet. — *Kosswigichthys asquamatus* ist endemisch in Anatolien.

3. *A. dispar*, *fasciatus* und *iberus* einerseits und *cypris* und *sophiae* andererseits bilden innerhalb der Gattung *Aphanius* zwei systematisch und ökologisch wohldefinierte Gruppen. In der ersten Gruppe sind auch Hybriden erzielt worden (reziprok, *fasciatus* \times *iberus*); Küstenwanderungen, Vorliebe für Salinen, Fortpflanzungsbereitschaft bei starker Salzkonzentration sind den Arten gemeinsam. *A. dispar* zeichnet sich durch ausgesprochene Thermophilie aus. — *A. cypris* und *sophiae* sind einander so ähnlich, daß sie nicht einwandfrei unterschieden werden können. Ökologisch betrachtet können in der Gruppe euryhalin-thermophile Populationen von Süßwasser und niedere Temperaturen vorziehenden getrennt werden. — *A. chantrei* und *burduricus* bilden eine dritte Gruppe, deren bemerkenswerte genetische Beziehungen gegenwärtig (durch Kosswig) bearbeitet werden. — *Tellia apoda* steht der erstgenannten *Aphanius*-Gruppe genetisch nahe.

Valencia ist unzureichend bekannt. — *Kosswigichthys* wird z. Z. ebenfalls einer genetischen Analyse unterzogen (Kosswig).

4. Die fossilen Vertreter der Cyprinodontiden in dem besprochenen Gebiete werden teils zu der rezenten Gattung *Cyprinodon*, teils zu den ausgestorbenen Gattungen *Prolebias*, *Pachylebias* und *Brachylebias* gezählt. Die 17 fossilen Arten finden sich im Tertiär (Oligozän und Miozän) von Frankreich, Südwest-Deutschland und Italien im Westen und von Persien im Osten.

5. Zoogeographische, ökologische und paläontologische Erwägungen machen es wahrscheinlich, daß die erwähnten Cyprinodontiden Tethys-Relikte sind. Die Gattung *Aphanius* mit ihrer heutigen mediterranen und indo-erythraischen Verbreitung muß bereits in der Tethys existiert haben. Das gleiche gilt für ihre Art *dispar*. *Fasciatus* dagegen dürfte jünger und könnte ein *dispar*-Abkömmling sein. *Iberus* kann gleichfalls als *dispar*-Abkömmling oder als noch jüngerer *fasciatus*-Abkömmling aufgefaßt werden. *Tellia* dürfte von der *dispar*-Gruppe herzuleiten sein, möglicherweise von *fasciatus* oder *iberus*. — Der Stammvater der *cypris*-Gruppe dürfte weiter verbreitet gewesen sein als die rezente Gruppe, jedoch weniger weit als der *dispar*-Gruppe. — Die *chantrei*-Gruppe und *Anatolichthys* werden in diesem Zusammenhang nicht diskutiert. — Die Fundulinae sind seit der Tethys wahrscheinlich in Verbreitung und Artenzahl zurückgegangen. Der hochspezialisierte *Kosswigichthys* dürfte ohne Frage jünger als die relativ primitive *Valencia* sein. Die Cyprinodontinae wiesen mit ihren sich weiter aufspaltenden Arten erhebliche Fortschritte auf. Ihre Artbildung vollzog sich in drei Stufen: die erste (Tethysstufe) umfaßte u. a. die Differenzierung von *A. dispar* und dem *A. cypris-sophia*-Ahnen; in der zweiten (Mittelmeer-Stufe) spalteten sich *fasciatus* und *iberus* ab; in der dritten

(Kontinental-Stufe) bildeten sich die zahlreichen Formen der *cypris-sophia*-Gruppe, die Inlandsform von *dispar* und vielleicht *T. apoda*. Obwohl geographisch getrennt, dürften sich die zweite und dritte Stufe zeitlich wenigstens teilweise überdecken.

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